

ETHOLOGY OF *HOLCOCEPHALA FUSCA* IN VIRGINIA (DIPTERA: ASILIDAE)

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Abstract.—*Holcocephala fusca* Bromley foraged primarily from twig tips on the edges of forest clearings. Prey were captured and immobilized in flight. The preferred prey consisted of Hymenoptera and Diptera. While in copula the male assumed a position similar to that observed in *Leptogaster* spp., with his head down and dorsal surface facing the same way as the female's ventral surface. Collected eggs had hexagonal sculpturing on the chorion. Grooming behavior and nocturnal resting position are similar to that described for other species of Asilidae.

In the United States there are three described species in the robber fly genus *Holcocephala* (Martin, 1965): *H. abdominalis* (Say), *H. calva* (Loew), and *H. fusca* Bromley. To date only the ethology of *H. abdominalis* has been described in some detail (Johnson, 1976) and limited ecological observations have been made for the other two species.

The present paper adds to our knowledge of the ethology and ecology of *H. fusca*. This species was studied intermittently for a two week period from August 21 to September 5, 1976, in a forested area in Fairfax, Virginia, at an elevation of approximately 152 m above sea level. The habitat consisted of a mixed stand of pine (*Pinus* sp.), oak (*Quercus* sp.) and a few hickory (*Carya* sp.) trees, with a dense shrub understory of blackberry (*Rubus* sp.), greenbrier (*Smilax* sp.), and rose (*Rosa* sp.). *Holcocephala fusca* were mostly found on the edge of the forested area near its juncture with lawn areas of apartment buildings. A few asilids were also observed on the edge of small clearings in the forest, but they seemed to prefer and were most abundant near large, open areas. This species was never observed in the darker more thickly vegetated areas of the forest. Both *H. abdominalis* and *H. calva* have generally been reported to occur in moist edges of meadows, woodland areas and marshy lakes which contain sedges

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and grasses (Baker and Fischer, 1975; Brimley, 1922; Bromley, 1931, 1946, 1950a, 1950b; Hull, 1962; McAtee and Banks, 1920). Scarbrough (1974) reported these species to occur in dry fields composed of shrubs and trees, a stream margin in a wood-field and along a sunlit path in some woods. Also, Johnson (1976) found *H. abdominalis* to occur in an open field. It is of interest to note that when *H. abdominalis* and *H. calva* occurred simultaneously within a habitat, *H. calva* were far less numerous (Baker and Fischer, 1975; Bromley, 1931; McAtee and Banks, 1920). This may indicate that interspecific competition can keep *H. calva* populations at relatively low levels.

RESTING BEHAVIOR

Holcocephala fusca rested on the vegetation in the shade or sun, with its body parallel to the ground or the twig it was on, or with its body at a 45° angle to the vertical like *H. abdominalis* (Johnson, 1976). The asilids almost always faced open areas where there was lower growing vegetation than their resting place. Also, they rarely faced areas shaded by vegetation, but faced sunlit areas or directly into the sun. This position presumably made it easier to see the outline of their prey. Melin (1923) stated that asilids "... often catch their prey against the sun ...". A few non-foraging individuals, mostly males, were observed on twig tips 230 cm above the ground. These males were usually "resting" between searching flights for receptive females with which to mate. *Holcocephala fusca* were never observed to land on the ground.

FORAGING AND FEEDING BEHAVIOR

Holcocephala fusca generally foraged from the tips of vegetation (mostly blackberry and rose twig tips) 30 to 120 cm above the ground. However, when the wind blew in excess of 3.2 km/hr the asilids moved closer to the ground and foraged at heights between 7.5 and 60 cm above the ground.

During flight *H. fusca* held their fore legs in a modified "chair-like" position up against the body, slightly extended, and bent between the femora and tibia. The mid and hind legs were held in a similar position, but with the femora at a 60° to 90° angle to the body and a more pronounced bend between the femora and tibia. A similar positioning of the legs has been reported for *H. abdominalis* (Johnson, 1976) and *Leptogaster* spp. (Dennis and Lavigne, 1976b; Hobby, 1931a; Melin, 1923; Parmenter, 1952; Scarbrough and Sipes, 1973; Seguy, 1950).

As has been reported for other species of Asilidae (Dennis and Lavigne, 1975), *H. fusca* would often make several forage flights from the same twig tip before changing its foraging site. Then they would generally fly 60 to 90 cm to another location and resume foraging.

While this species was engaged in foraging activity and while it was feed-

ing, it continued to observe other insects, as indicated by rapid movements of its head and body. According to Melin (1923), these movements allow asilids to obtain a larger field of vision. In addition, it probably allows them to see their prey with the central ommatidia of their eyes. Melin demonstrated that these ommatidia probably have a greater intensity of vision than the surrounding ommatidia.

Holcocephala fusca usually made forage flights and captured prey in sunlit areas, although a few prey were captured in the shade of vegetation. Forage flights into sunlit areas were for distances of 12.5 to 90 cm, whereas forage flights into shaded areas were much shorter (usually 12.5 to 30 cm). It is assumed that the asilids made longer forage flights in sunlit areas because of increased visual acuity.

Although forage flights were made for distances up to approximately 90 cm from an asilid's foraging position, prey were observed to be successfully captured only within 12.5 to 30 cm of the asilid. Like *H. abdominalis* (Johnson, 1976), all prey were captured in the air either to the side or in front of an asilid. However, most prey were captured directly in front of the asilid and 10 to 15 cm above its foraging position. It is assumed that the manner in which *H. fusca* carried its legs in flight enabled it to more readily capture its prey. The positioning of the legs in flight has also been associated with prey capturing methods of *Leptogaster* (Dennis and Lavigne, 1976b; Martin, 1968; Melin, 1923).

Holcocephala fusca made frequent forage and investigatory flights. During the latter type flights the asilids would either chase insects without coming into contact with them, or make contact with potential prey, manipulate them with all six tarsi and then release them. According to Dennis and Lavigne (1975), investigatory flights probably help asilids discriminate between suitable and unsuitable prey before actually attacking. Also, asilids which release prey may have poorer powers of vision than asilids which capture prey and do not release them. However, it is possible that prey may be rejected for other reasons, such as odor or toughness of the integument (e.g., Coleoptera).

Holcocephala fusca made frontal captures which resulted in the prey's head being directly underneath the asilid's head following capture. Once prey were captured, the asilid would either immediately insert its hypopharynx or manipulate the prey with all six tarsi for 15 to 25 seconds before insertion. During manipulation the asilid would often move 30 to 90 cm from the capture site before landing to feed. The hypopharynx was always observed to be inserted into the dorsum of the prey's thorax or in the intersegmental membrane between the head and thorax. These points of insertion are the ones most frequently reported in the literature. Johnson (1976) observed that *H. abdominalis* also inserted its hypopharynx in the mouth and anus of Formicidae.

Not all prey were immobilized as soon as the asilid inserted its hypopharynx. Prey, in particular Formicidae, often remained active for 20 to 25 seconds before being completely immobilized. This may have resulted from the hypopharynx either not penetrating a ganglion or not being inserted close enough to one of the anterior nerve centers. In addition, *H. fusca* and asilids in general, may be able to regulate the amount of neurotoxin which is injected into prey and small amounts may not immobilize prey as fast as large amounts.

After prey were captured, *H. fusca* often returned to its previous foraging site. If this position was in a sunlit area, they would then frequently move into a shaded area where the temperature was 2 to 3°C lower than that in the sun. Lavigne and Dennis (1975) observed that such behavior probably helps asilids maintain their normal body temperature by reducing exposure to the sun's rays.

As *H. fusca* fed, prey were manipulated with all six legs as the asilid hovered 7.5 to 10 cm around its feeding station. The hypopharynx was removed and reinserted during the hover after which the asilid settled down and continued feeding. Hovers generally lasted for 7 to 8 seconds and during this period the asilid often moved 30 to 90 cm from its former feeding position before settling down. It is of interest to note that prey manipulation was rarely observed, possibly because the small size of the prey did not necessitate it. Johnson (1976) never observed *H. abdominalis* to manipulate prey and also speculated that this was due to the small size of the prey. Hovering and manipulating prey has been observed quite frequently in the subfamily Asilinae, but not in the Dasypogoninae, to which *H. fusca* belongs (Dennis and Lavigne, 1975; Lavigne and Holland, 1969).

During feeding prey were allowed to hang free and were frequently observed to balloon. However, like *H. abdominalis* (Johnson, 1976), abdominal pumping by *H. fusca* was never observed. Prey ballooning has been attributed to asilids pumping digestive enzymes and digested material in and out of the prey (Lavigne and Holland, 1969).

Holcocephala fusca fed on prey for an average of 10 minutes 54 seconds with a range between 1 minute and 29 minutes 30 seconds. There was a positive correlation between the time spent feeding and the length of the prey. Prey with an average length of 1.25 mm, such as *Bradysia* sp., were fed on for approximately 9 minutes 30 seconds; whereas winged reproductive *Myrmecina americana* Emery, which averaged 3.0 mm in length, were fed on for 20 to 24 minutes.

At the completion of feeding prey were usually pushed off of the asilid's hypopharynx with the fore tarsi. However, some prey were discarded as the asilid withdrew its hypopharynx without touching the prey. Some prey were also allowed to drop off the asilid's hypopharynx as it flew to a new location, began to forage for other prey or captured another prey. Johnson

Table 1. Relation between length of *Holcocephala fusca* and that of its prey.

Sex	Predator Length (mm) ^a			Prey Length (mm)			No. of Prey Measured	Mean Ratio of Predator to Prey
	Minimum	Maximum	Mean	Minimum	Maximum	Mean		
Male	5.0	6.5	5.9	0.5	3.0	1.5	27	3.9
Female	5.0	7.0	5.9	0.5	3.5	1.9	77	3.1
Unidentified ^b	—	—	—	3.0	3.0	3.0	1	—
Total	5.0	7.0	5.9	0.5	3.5	1.7	105	3.5

^a 10 predators of each sex were measured.

^b Unidentified indicates that the sex of the predator was not determined.

(1976) observed *H. abdominalis* to always discard prey at the completion of feeding by pushing prey off its hypopharynx with its fore tarsi.

The time between feedings (interfeeding time) varied between 0 and 22 minutes 30 seconds, with an average of 9 minutes 42 seconds. The 0 minute interfeeding time was for flies which dropped prey they were feeding on and immediately captured another victim.

As with other species of Asilidae, it is possible to calculate the theoretical number of prey an individual *H. fusca* could feed on in one day if one assumes, (1) the asilid continually engages in foraging and feeding between 10:30 AM and 7:30 PM (the observed major period of foraging and feeding activity), and (2) the asilid captures and feeds on one prey every 20 minutes 36 seconds (based on the average feeding and interfeeding times). Thus, over a 9 hour period this species could feed on approximately 26 prey per day. Other investigators have estimated that asilids feed on from 4 to 35 prey per day (Dennis and Lavigne, 1975, 1976a, 1976b; Lehr, 1964).

Table 2. Number and percent composition of different orders of prey taken by *Holcocephala fusca*.

Order	Male		Female		Total	
	Number	Percent	Number	Percent	Number	Percent
Coleoptera	1	3.2	9	10.1	10	8.2
Diptera	18	58.1	33	37.1	51	41.8
Hemiptera	0	0.0	1	1.1	1	0.8
Homoptera	6.5	1	1.1	3	2.5	2
Hymenoptera	10	32.3	39	43.8	51 ^a	41.8
Lepidoptera	0	0.0	1	1.1	1	0.8
Psocoptera	0	0.0	5	5.6	5	4.1
TOTAL	31		89		122 ^a	

^a Includes two Hymenoptera for which the predator sex is unknown.

The mean predator to prey size ratio for this species is 3.5 (Table 1). Both male and female *H. fusca* had the same mean length, however, females caught larger prey. Thus, females have a smaller mean predator to prey size ratio than do males (i.e., 3.1 and 3.9, respectively).

Holcocephala fusca appears to be fairly selective in its choice of prey. Diptera and Hymenoptera made up approximately 84 percent of the total number of prey (Table 2). Coleoptera, Hemiptera, Homoptera, Lepidoptera and Psocoptera made up 8.2, 0.8, 2.5, 0.8 and 4.1 percent of the prey, respectively. Females preyed on insects from seven orders, whereas males preyed on insects from only five orders. Both males and females preyed on similar species within an order, however males seemed to prefer Diptera (58.1 percent) and females preyed more heavily on Hymenoptera (43.8 percent). *Holcocephala abdominalis* has also been reported to feed primarily on Hymenoptera and Diptera (Bromley, 1950b; Johnson, 1976; McAtee and Banks, 1920). Johnson (1976) found that both sexes of *H. abdominalis* fed on approximately the same percentage of prey belonging to these two orders.

As has been reported for other species of Asilidae (Dennis and Lavigne, 1975; Hobby, 1931a, 1931b; Lavigne, 1970; Lehr, 1958a, 1958b; Poulton, 1906; Richards, 1927), more females were captured with prey than males. This phenomenon has been attributed to, (1) the female's need for additional nourishment for development of her eggs (Hobby, 1931a), (2) males spending less time foraging and feeding, and more time searching for and mating with females, (3) in some populations of asilids there may be more females than males, and (4) females may have shorter feeding and interfeeding times and thus catch more prey than males (Dennis and Lavigne, 1975).

The following is a list of prey taken by *H. fusca*. All prey were collected in Fairfax, Virginia, between August 21 and September 5, 1976, by capturing the asilids in a baby food jar. In some instances prey are identified only to the family or subfamily level since specific identifications are not available. D. M. Anderson (Scolytidae), R. J. Gagné (Cecidomyiidae, Sciaridae), G. Gordh (Aphelinidae, Encyrtidae, Eulophidae, Eupelmidae, Pteromalidae), R. D. Gordon (Orthoperidae), J. L. Herring (Anthocoridae), J. M. Kingsolver (Cryptophagidae, Languriidae, Ptilidae), P. M. Marsh (Ceraphronidae, Scelionidae), A. S. Menke (Cynipidae), C. W. Sabrosky (Anthomyzidae, Chloropidae), D. R. Smith (Formicidae), G. Steyskal (Sphaeroceridae), M. B. Stoetzel (Aphididae, Aleyrodidae), F. C. Thompson (Dolichopodidae, Simuliidae), R. White (Chrysomelidae), and W. W. Wirth (Ceratopogonidae, Chironomidae, Phoridae) of the Systematic Entomology Laboratory, IIBIII, Agric. Res., Sci. and Educ. Admin., USDA, Washington, D.C. and Beltsville, Maryland, D. R. Davis (Gracillariidae) of the National Museum of Natural History, Smithsonian Institution, Washington, D.C., and E. L. Mockford (Ectopsocidae, Psocidae) of the Illinois State University, Normal,

Illinois, are thanked for the prompt identification of their respective groups. The number and sex (if known) of the predator is indicated in parentheses following the prey record.

COLEOPTERA, Chrysomelidae: *Chaetocnema* sp. prob. *pulicaria* Melsheimer, IX-4-76 (♀); Cryptophagidae: *Anchicera* sp., VIII-21-76 (♀); Languriidae: *Corticaria* sp., IX-4-76 (2 ♀); Orthoperidae: *Orthoperus* sp., VIII-22-76 (♀, ♂); Ptilidae: *Achratrichis* sp., VIII-21-76 (♀); Scolytidae: *Pityophthorus* sp. nr. *rhois* Swaine, VIII-22-76 (♀); Staphylinidae: Unidentified, VIII-21-76 (♀), VIII-30-76 (♀). DIPTERA, Anthomyzidae: *Anthomyza* sp., IX-4-76 (♂); Cecidomyiidae: *Cecidomyia piniinopsis* O.S., VIII-30-76 (♂), *Clinodiplosis* sp., VIII-22-76 (♂), *Dasineura* sp., VIII-22-76 (♂), *Lesiodiplosis* spp., VIII-21-76 (♀), VIII-22-76 (♂), VIII-29-76 (2 ♀), VIII-30-76 (♂), *Neolasioptera* sp., VIII-22-76 (♀), *Peromyia* sp., VIII-22-76 (2 ♀, ♂), *Porricondyla* sp., VIII-30-76 (♀); Ceratopogonidae: *Culicoides paraensis* (Goeldi), VIII-21-76 (♀); Chironomidae: *Cricotopus* sp., VIII-22-76 (♀), Orthoclaadiinae, VII-22-76 (♂); Chloropidae: *Monochaetoscinella nigricornis* (Lw.), VIII-21-76 (2 ♀), VIII-22-76 (♀, ♂), *Oscinella umbrosa* (Lw.), VIII-21-76 (♀); Dolichopodidae: *Chrysotus* sp., VIII-30-76 (♀, ♂); Phoridae: *Megaselia* sp., VIII-21-76 (♀), *Puliciphora* sp., VIII-21-76 (♂), VIII-22-76 (♀); Sciaridae: *Bradysia* sp., VIII-21-76 (♀, ♂), VIII-22-76 (♀, 3 ♂), VIII-29-76 (♀), VIII-30-76 (♀, ♂), IX-4-76 (2 ♀), IX-5-76 (♂); Simuliidae: *Simulium (Phosterodoros)* sp., VIII-21-76 (3 ♀), VIII-22-76 (4 ♀, ♂); Sphaeroceridae: *Leptocera* sp., VIII-22-76 (2 ♀), IX-4-76 (♀); unidentified VIII-21-76 (♀). HEMIPTERA, Anthocoridae: *Orius insidiosus* (Say), VIII-22-76 (♀). HOMOPTERA, Aleyrodidae: Unidentified, VIII-22-76 (♂), IX-4-76 (♀); Aphididae: *Cinara* sp., VIII-29-76 (♂). HYMENOPTERA, Aphelinidae: Unidentified, IX-5-76 (♀); Ceraphronidae: *Ceraphron* sp., IX-4-76 (♀); Cynipidae: Eucoilinae, VIII-21-76 (♀), *Kleidotoma* sp., VIII-22-76 (♀); Encyrtidae: *Copidosoma* sp., VIII-29-76 (♂), IX-5-76 (♀), *Tachinaephagus zealandicus* Ashmead, VIII-21-76 (♀), VIII-22-76 (♀), IX-4-76 (♀); Eulophidae: *Tetrastichus* sp., VIII-21-76 (♀); Eupelmidae: *Lutnes* sp., IX-4-76 (♀); Formicidae: *Lasius* sp., VIII-21-76 (♀), *Myrmecina americana* Emery, VIII-21-76 (♀), VIII-22-76 (8 ♀, 1 ♂, 1 no sex), VIII-29-76 (11 ♀), IX-4-76 (3 ♀, 2 ♂), IX-5-76 (2 ♀, 2 ♂, 1 no sex), *Ponera pennsylvanica* Buckley, VIII-22-76 (2 ♂), VIII-29-76 (♀); Pteromalidae: *Eupteromalus* sp., VIII-30-76 (♂), *Halticoptera* sp., VIII-21-76 (♀); Scelionidae: *Telenomus* sp. (?), VII-22-76 (♂), *Trimorus* sp., IX-4-76 (♀). LEPIDOPTERA, Gracillariidae: *Phyllonorycter* sp., VIII-21-76 (♀). PSOCOPTERA, Ectopsocidae: *Ectopsocopsis cryptomeriae* (Enderlein), VIII-22-76 (♀), IX-4-76 (3 ♀), *Trichadenotecnum alexanderiae* Somm., VIII-21-76 (♀).

Bromley (1950b) recorded *H. fusca* as preying upon *Culicoides* spp., *Phortica* sp., and a scolytid beetle.

While in the baby food jar *H. fusca* frequently exhibited thanotosis or lay

on their dorsum with one or both wings spread and kicked their legs. Dennis and Lavigne (1975) reported that several species of asilids they studied exhibited thanotosis. Also, as has been reported for *Leptogaster parvoclava* (Dennis and Lavigne, 1976b), one male of *H. fusca* dropped its prey off its hypopharynx and carried the prey around in its hind tarsi as it tried to escape from the jar.

MATING BEHAVIOR

The only behavior associated with premating exhibited by *H. fusca* was male searching flights. These flights consisted of the males flying in an irregular path 60 to 240 cm above the ground for periods of 25 to 120 seconds. In flight the males' legs were held in a position similar to that of foraging *H. fusca*. As the males searched for receptive females with which to mate they frequently hovered in front of seeds on vegetation and briefly landed on rose or greenbrier thorns. However, males were never observed to hover in front of females or exhibit a more complex type of courtship. This is in sharp contrast to the apparent courtship behavior of *H. abdominalis*. Johnson (1976) reported that the males of this species hover in front of females, but without any obvious epigamic display (i.e., signaling with the legs).

In addition to briefly landing on inanimate objects during searching flights, males frequently landed on other males and females. A male would locate another asilid, land on its dorsum facing the same direction, curve his abdomen to the right or left of the asilid's abdomen, and then try to clasp the asilid's genitalia from below. When a male or a non-receptive female was contacted, the asilids would avoid mating by raising and spreading their wings over their dorsum, curve their abdomen down, and kick at or push the male away with their hind legs. Non-receptive asilids also frequently held their hind legs up behind their wings in order to prevent males from landing on them. These agonistic postures were performed even when a male was hovering over a non-receptive asilid, thus making it physically impossible for the male to land on the asilid. Mating attempts were also discouraged when the accosted asilids flew off, flattened themselves against or crawled around the vegetation. Males exhibited this behavior more frequently than wing spreading. Similar agonistic postures and methods of avoiding copulation have been observed for *H. abdominalis* (Johnson, 1976) and other species of Asilidae (Dennis and Lavigne, 1975, 1976b).

Males often attempted to mate several times with the same asilid before resuming their searching flights. In addition, they attempted to mate with asilids which were feeding on prey, as well as those engaged in foraging or resting on vegetation.

No complete matings were seen and only two mating pairs were observed. Both pairs were approximately 1 m above the ground on vegetation at 3:03.5 PM and 5:00 PM when the air temperature at the asilid's height were 31.5

and 29°C, respectively. The latter mating pair were in the shade where it was approximately 2°C cooler than in a nearby sunlit area.

This species assumed a mating position quite similar to that of *H. abdominalis* (Johnson, 1976) and *Leptogaster* spp. (Dennis and Lavigne, 1976b; Melin, 1923; Scarbrough and Sipes, 1973). Females held onto vegetation while the males hung free in a head down position with their wings folded over their dorsum and their dorsal surface facing the same direction as did the females' ventral surface. The female of one mating pair held onto the vegetation with the fore and mid legs while the hind legs hung free. While in this position, the female frequently kicked her hind legs or rubbed both abdomens and genitalia with her hind legs. Males of both mating pairs held their legs up against their body or slightly extended.

One mating pair was lost to sight when they flew into the forest after being observed for 4 minutes. The other mating pair was observed to fall onto vegetation on the ground and separate, after being watched for only 30 seconds. The female then flew back to the twig tip where mating had occurred and the male flew onto vegetation 10 to 12 cm above the ground.

OVIPOSITION

Oviposition by female *H. fusca* has not been observed. However, since their genitalia do not have apical spines it is assumed that this species oviposits in or on vegetation, or that they drop their eggs while resting on vegetation or while in flight, as has been observed for *Leptogaster* spp. (Bromley, 1946; Dennis and Lavigne, 1976b; Melin, 1923; Parmenter, 1952; Scarbrough and Sipes, 1973; Skidmore, 1966). Johnson (1976) speculates that *H. abdominalis* females oviposit by broadcasting the eggs during flight. According to Melin (1923), asilids like *H. fusca* which have yellow or brownish eggs, drop their eggs in flight or deposit them in open hiding places.

Eggs of *H. fusca* were collected from two females which oviposited in vials. One female deposited 3 eggs in a vial and the other female deposited 46 eggs. The eggs were quite similar in appearance to those of *H. abdominalis* (Johnson, 1976) and *Leptogaster* spp. (Dennis and Lavigne, 1976b; Lavigne, 1963; Melin, 1923; Newkirk, 1963; Parmenter, 1952; Scarbrough and Sipes, 1973; Skidmore, 1966) (Fig. 1). All eggs were a light to dark amber. At 100× hexagonal sculpturing was easily visible on the chorion where the yolk material had pulled away from the chorion. The yolk material at the same magnification appeared to consist of a gelatinous-fibrous or granular material. The eggs were slightly oval with an average width and length of 0.175 and 0.263 mm, respectively. The range in width was from 0.160 to 0.184 mm and the range in length was from 0.240 to 0.280 mm. All asilid eggs which have been described in the literature are oval or oblong, however, chorionic sculpturing has not been frequently reported. According

to Parmenter (1952) asilid eggs may have bumps or ridges, but they lack fine sculpturing like that found on Lepidoptera eggs. Melin (1923) reported that *Laphria* spp. and *Dioctria* spp. have eggs with "facet-like ridges" and diagrammed part of an egg with five-sided ridges. Scarbrough (1978) found similar ridges on the eggs of *Cerotainia albipilosa* Curran and Johnson (1976) observed pentagonal and hexagonal sculpturing on the eggs of *Holcocephala abdominalis*.

GROOMING

All Asilidae studied to date appear to groom in much the same way, with species specific variations in the sequence and relative frequency of grooming (Dennis and Lavigne, 1975, 1976b). *Holcocephala fusca*, evidently like *H. abdominalis* (Johnson, 1976), spent more time grooming its wings, abdomen, and hind legs. The only time they generally groomed their fore legs and face was immediately after feeding. This species typically rubbed its fore and hind tarsi together before grooming its face and abdomen (this includes the wings), respectively. After rubbing the hind tarsi together *H. fusca* would groom the abdomen and wings with one or both hind tarsi from anterior to posterior. Oftentimes the abdomen was curved downward during grooming and one wing or side of the abdomen was then groomed. When the asilids groomed one side at a time they appeared to be scratching themselves. *Leptogaster parvoclava* has also been observed to groom one wing at a time while the wing is bent downward, at a right angle to its body (Dennis and Lavigne, 1976b). Most Asilidae however appear to groom both wings simultaneously.

NOCTURNAL RESTING POSITION

Holcocephala fusca typically began settling down for the night when the entire study area was enveloped in shade. This generally occurred at approximately 7:45 PM. At this time the asilids became less active and most of them merely stood up on all six legs on twig tips. Within 15 to 20 minutes the asilids made stepping movements with their legs and then flattened themselves against the twig tips or moved backwards 1 to 3.5 cm and flattened themselves against the top or side of the twig. They remained in this position throughout the night.

COMPARATIVE BEHAVIOR OF ASILIDAE

Throughout this paper and in other publications on Asilidae (in particular those by Dennis and Lavigne, 1975, 1976a, 1976b; Lavigne and Holland, 1969; Melin, 1923) emphasis has been placed on comparing behavior patterns and other characteristics of species in the same genera and subfamilies. As more species are studied it is becoming evident that taxonomically related species have similar behavior patterns. However, these species can be

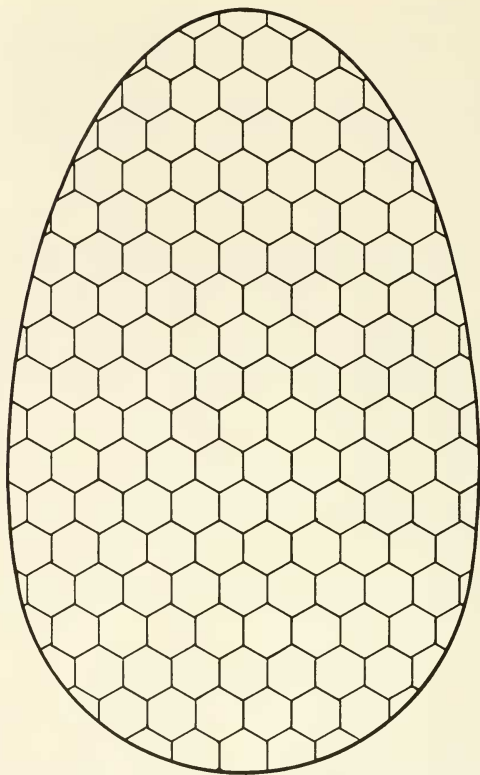


Fig. 1. Diagrammatic representation of egg of *Holcocephala fusca* (approximately 470 $\times$ normal egg size).

distinguished by slight variations in their behavior, such as the methods of prey manipulation or oviposition.

It is hoped that ultimately studies of asilid behavior will yield information on the evolutionary trends of morphological characteristics, which may in turn reveal phylogenetic relationships of various taxa. This may be particularly useful in determining the validity of the family status given the subfamily Leptogastrinae by Martin (1968). Martin proposed to give this group family status based on certain morphological and behavioral characteristics. However, comparative data for *Holcocephala* spp. (*Dasypogoni-*

nae) and *Leptogaster* spp. (Leptogastrinae) presented in this paper, indicate the possibility of a close phylogenetic relationship between the Leptogastrinae and other asilid species. For example, the eggs of many asilids are oblong and white; whereas, the eggs of *Leptogaster* and *Holcocephala* are oval or semi-oval and amber or yellowish brown (the eggs of *Dioctria* spp. are also semi-oval and reddish brown, Melin, 1923). Both *Leptogaster* and *Holcocephala* hold at least their fore legs in front of their body during flight, other asilids hold the legs under their body. In addition, these two genera have a similar mating position not reported for other genera of Asilidae. The female rests in a position vertical to the ground on vegetation, while the male hangs free or else supports himself below on vegetation with his dorsal surface facing the same way as the female's ventral surface. In other asilids the two sexes are either facing the same direction with the male remaining on top of the female (male over female position), or they face in opposite directions with their dorsal surfaces facing the same direction (tail-to-tail position).

Certainly more than the aforementioned characteristics are needed before such information can be used for taxonomic purposes. However, more detailed ethological and ecological observations should help clarify the present system of classifying Asilidae and related groups, which is based primarily on morphological characteristics.

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